

THE BIOLOGY OF CEPHALODESMIUS, A GENUS OF DUNG BEETLES
WHICH SYNTHESIZES “DUNG” FROM PLANT MATERIAL
(COLEOPTERA:SCARABAEIDAE:SCARABAEINAE).

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ABSTRACT

The complex and aberrant biology of the endemic, Australian dung beetle genus, *Cephalodesmius*, is described from a detailed study of *C. armiger* and supporting observations on the other two species of the genus, *C. laticollis* and *C. quadridens*. Permanently bonded pairs occupy fixed, subterranean nests in the rainforest floor during their year-long lifespan. Males forage outside the nest for leaves and other plant materials which are processed and cultured by the female into a malleable, dung-like material which is used to construct small brood balls containing larvae. During larval growth the parent beetles cooperate in progressive provisioning of the larval brood balls, a complexity unknown elsewhere in the dung beetles and probably unique in the Coleoptera. Audible stridulation is recorded for the first time in larval Scarabaeidae, and a new mechanism of sound production described in which the tip of the abdomen is rubbed against the underside of the head. Stridulation is interpreted as communication between larva and adult.

The brood nests of *Cephalodesmius* are inhabited by a suite of 8 other insects and mites which enter into a variety of trophic and phoretic relationships with the beetles and these are summarized. The evolutionary significance of the behaviour of *Cephalodesmius* is discussed.

INTRODUCTION

The subfamily Scarabaeinae is a large, diverse and successful group which has earned the common name of ‘dung beetles’ through their almost universal utilization of animal dung as larval and adult food. Although a few species are known to feed on other diets such as fruits, carrion, feathers and fungi it is generally accepted that dung is the primitive and primary food of the subfamily. The classic observations of J.H. Fabre (1897) were the first to reveal that some dung beetles have complex behaviour patterns by which they manipulate and transport dung to subterranean nests where they rear their immature stages. It is now known that there is a remarkable array of variations on the basic breeding behaviour described by Fabre, that of some species approaching the most intricate known in the Insecta. Halffter and Matthews (1966) give a comprehensive review and analysis of the overall

biology of the world fauna, while Halffter (1977) gives a comparative account of nesting behaviour (nidification) in the subfamily, including possible evolutionary pathways.

The six tribes of Scarabaeinae show a basic behavioural dichotomy into (i) those that bury the dung in preformed burrows at the food source (Onthophagini, Oniticellini, Onitini and Coprini), and (ii) those that form the dung into balls which are transported away and buried at a distance from the source (Scarabaeini and Eurysternini) (Halffter, 1977). The latter group are often termed ‘ball-rollers’. All Australian ball-rollers belong to the tribe Scarabaeini and have been comprehensively revised by Matthews (1974) who placed all 16 genera into the primitive, Gondwana subtribe, Canthonina. Matthews notes that 11 genera of the Australian Canthonina, comprising what he terms the ‘mentophiline-group’, have not been observed to make balls and he suggests they represent an early evolutionary stage before the

acquisition of this ability in the Scarabaeini. He draws attention to the paucity of information on the biology of these 'mentophilines' and suggests such data might throw light on the evolution of behaviour in dung beetles.

One of these mentophilines is *Cephalodesmius* Westwood, an endemic Australian genus with three flightless species restricted to wetter forests of SE Queensland and N.S.W. All three species are common insects where they occur. *Cephalodesmius laticollis* Pascoe and *C. quadridens* Macleay are confined to the northern part of the generic range, while *C. armiger* Westwood is virtually ubiquitous in rainforests and some adjacent sclerophyll forests throughout the range of the genus from the Bunya Mountains south to Wollongong. All three species overlap in the Macpherson Range complex on the N.S.W./Qld border.

Previous observations on the biology of *Cephalodesmius* are fragmentary and somewhat conflicting. Fricke (1967) excavated a burrow near Sydney to find a pair of adult *C. armiger*, a large, oval pellet of what he took to be horse dung, and 5 smaller pellets. He kept the pellets in a container with the adults during which time they consumed part of the 'horse dung' and tended the round pellets. Eventually an adult emerged from one pellet and the others, when opened, contained dead larvae and pupae. Matthews (1974) records his personal observations of *armiger* digging short burrows in captivity, and of both *armiger* and *laticollis* shaping rough balls of dung which they dragged backwards instead of rolling; he also notes an 'extraordinary observation' by G.B. Monteith who reported *C. quadridens* 'in holes filled with pieces of green leaves under logs' at the Bunya Mountains. Finally, a most important early observation, overlooked by other writers but brought to our notice by Dr B.P. Moore, is that of Walker (1905, p. 269) who writes:

'The curious small Coprid, *Cephalodesmius armiger* Westwood, is also somewhat diurnal in its habits. In the Illawarra in April, 1903, I found the females of this beetle busily engaged in filling their burrows under the logs with fresh minced-up leaves of clover and other low-growing plants, presumably as food for the larvae; a habit which recalled to my recollection the proceedings of the still more singular *Lethrus*, which I had observed in Turkey many years ago provisioning its burrow with vine leaves.'

The major inconsistency in these isolated reports is the contrast between the apparently

normal association with dung seen by Fricke and Matthews, and the apparently abnormal association with leaf material noted by Walker and Monteith. Accordingly, a detailed field and laboratory study of the biology of *Cephalodesmius* was carried out during the period 1972-74 in an attempt to resolve this anomaly. The results of this study are presented in this paper. We know now that all the previous observations are indeed correct, except for the certainty that what Fricke saw was not 'horse dung' but plant material mashed by the beetles themselves. *Cephalodesmius* adults do, as noted by Matthews, feed on dung when the opportunity arises but most of their foraging activity goes into gathering leaves and other vegetable material which is mashed and cultured in preformed underground nests into a dung-like substance which forms the larval brood material and much of the adult diet. This remarkable adaptation is quite unique even in an enormous subfamily famous for its behavioural eccentricities. Other striking features of *Cephalodesmius* biology which emerge from this study include: permanent pair-bonding of males and females during a lifetime of almost 12 months; residence in a single burrow during the life of the pair; deposition of eggs in tiny 'egg-balls' which are progressively provisioned with brood material as the larvae inside feed and grow; and phoretic and trophic associations with a large suite of other organisms which share their nests.

Due to the delay in publication of this comprehensive account, certain aspects of our findings have been referred to, with our permission, in other papers dealing with related matters. These include Richards (1973) on phoretic flies, Matthews (1974) with footnotes on use of leaf material, Costa (1975) on phoretic mites, Hammond (1976) on phoretic staphylinids, Matthews (1976) with reference to leaf utilization, but erroneously citing eucalypt leaves, Halfpter (1977) who comments on the significance of *Cephalodesmius* to the evolution of nest behaviour in dung beetles, and Edmonds and Halfpter (1978) who refer to larval stridulation.

MATERIALS AND METHODS

This study is based on a detailed examination of the biology of *Cephalodesmius armiger*. This was supported by sufficient observations on *C. laticollis* and *C. quadridens* to confirm that all species of the genus have similar behaviour patterns. Studies on *C. armiger* took place in both field and laboratory.

TABLE 1: SUMMARY OF VISITS TO THE *CEPHALODESMIUS ARMIGER* STUDY SITE AT TOOLOOM PLATEAU AND THE COLLECTIONS MADE.

Visit No.	Date	Burrows excavated	Foraging beetles hand-collected	Beetles in pitfall traps since last visit
1	22 Oct. 1972	11	0	No trapping
2	4 Nov. 1972	5	0	No trapping
3	17 Dec. 1972	17	26♂ 0♀	No trapping
4	30 Dec. 1972	32	0	No trapping
5	30 Jan. 1973	9	0	No trapping
6	25 Feb. 1973	20	0	No trapping
7	25 Mar. 1973	12	0	No trapping
8	7 Apr. 1973	11	0	No trapping
9	10 Jun. 1973	21	0	No trapping
10	15 Jul. 1973	11	0	11♂ 5♀
11	5 Aug. 1973	25	0	12♂ 1♀
12	26 Aug. 1973	25	0	13♂ 1♀
13	16 Sept. 1973	9	0	18♂ 4♀
14	30 Sept. 1973	15	0	2♂ 3♀
15	21 Oct. 1973	11	0	6♂ 0♀
16	11 Nov. 1973	12	1♂ 0♀	16♂ 2♀
17	24 Nov. 1973	23	33♂ 1♀	5♂ 1♀
18	8 Dec. 1973	16	31♂ 4♀	1♂ 0♀
19	31 Dec. 1973	18	0	1♂ 0♀
20	19 Jan. 1974	16	0	2♂ 0♀
21	9 Feb. 1974	22	14♂ 20♀	5♂ 5♀
22	28 Feb. 1974	11	80♂ 10♀	1♂ 6♀
23	16 Mar. 1974	21	6♂ 24♀	3♂ 6♀
24	30 Mar. 1974	18	3♂ 11♀	4♂ 4♀
25	27 Apr. 1974	10	4♂ 4♀	4♂ 0♀
26	25 May 1974	11	0	1♂ 1♀
27	14 Jul. 1974	14	0	1♂ 0♀

FIELD STUDIES

The main study site was an area of subtropical rainforest on deep basaltic soil on the Tooloom Plateau in northern New South Wales (28° 29'S, 152° 31'E, Alt. 700 m). The site was chosen for its dense beetle population and its ready accessibility. It was visited 27 times between October 1972 and May 1974 (Table 1). Intervals between visits varied from 2–3 weeks in summer to 4–5 weeks in winter when beetle activity was slight. Each visit usually consisted of an overnight camp by one or both of the authors giving the opportunity for both diurnal and nocturnal observations. During visits one or more of the following activities was undertaken:

(i) **BURROW EXCAVATIONS:** From 10 to 30 burrows were carefully excavated using a flexible probe to follow the shaft from its surface opening to its terminal chamber. The structure of each nest was noted and the contents (beetles, brood mass, brood balls, foraged material, etc.) returned alive to the laboratory for closer study. In all 426 nests were thus excavated (Table 1).

(ii) **OBSERVATIONS AND COLLECTION OF FORAGING ADULTS.** Beetles emerging from their burrows to forage are large enough and slow enough for details of their behaviour to be readily observed with the naked eye. Day and night observations of any foraging activity were made on each visit. Items being carried by beetles were noted or collected for identification and associated phoretic organisms recorded. Samples of foraging beetles were collected into alcohol for sexing and age determination in the laboratory. (Table 1).

(iii) **PITFALL TRAPPING.** To monitor above-ground beetle activity between visits three large formalin-filled pitfall traps (2 gallon buckets) were installed between June 1973 and March 1974 and cleared at each visit. Beetles trapped were counted, aged and sexed (Table 1).

(iv) **BURROW DENSITY ESTIMATION.** On August 26, 1973 an estimate of *armiger* burrow density at the Tooloom study site was made by counting burrow entrances visible in 25 random 1 m² quadrats in each of two 1000 m² plots.

LABORATORY STUDIES

(i) PROCESSING OF CONTENTS OF EXCAVATED NESTS. The following details of nest contents were recorded: number and sex of adult beetles; presence and nature of brood mass and foraged material; number, size and contents (eggs, larvae or pupae) of brood balls; and presence of other organisms. From each batch of nests several females were dissected to ascertain the condition of developing eggs in the ovaries.

(ii) AGEING OF ADULTS. The highly synchronized 12 month life cycle of *Cephalodesmius* means that the whole population is roughly of the same age at a given time. However there is some overlap of two generations in late summer when the new generation is hatching from the nests. At this time samples of hand-collected or pitfall-collected foragers could be divided easily into old and new generation by the excessive wear on the clypeal prongs and tibial teeth of the surviving adults from the old generation.

(iii) ARTIFICIAL NEST STUDIES. To study the behaviour of *Cephalodesmius* inside their burrows pairs of beetles were excavated from field nests and set up in artificial laboratory nests. Initially, 'transect cages' as described by Bornemissza (1971) were experimented with. These are basically a layer of soil held between two sheets of glass. *Cephalodesmius* placed in such containers readily excavated burrows but observation was difficult due to soil adhering to the glass, and constant problems were encountered with maintenance of natural soil moisture. Hence, completely artificial nests were made from Plaster of Paris using plasticine models of the natural burrow configuration as moulds. Fitted with removable glass fronts these were highly successful and the beetles readily adapted to the complete lack of soil. Similar plaster nests have subsequently been used by Klemperer (1979) in studies of geotrupid beetles.

In the late winter of 1973 (July/August) 12 pairs of *Cephalodesmius armiger* and 3 pairs of *C. laticollis* were brought from the field and established in plaster nests; males were marked with paint for ease of recognition. They were regularly supplied with soft leaves (usually clover) and flowers (clover and hibiscus) which they readily carried down to the burrow chamber; some nests were also supplied with dung. These pairs survived in the nests for up to two months during which time they manufactured brood material, formed egg balls and commenced progressive

provisioning of larval balls. Activity was viewed through the glass front which could be temporarily removed to permit photography or inspection of nest contents. All nests eventually died out in the larval stage due to invasions of mites and fungi, and an apparent decline of vigor in the laboratory. The sequence of events observed in the plaster nests is summarized in Fig. 10.

RESULTS

OBSERVATIONS ON *CEPHALODESMIUS ARMIGER*

The annual cycle of activity of this species is indicated by Fig. 1 which gives a summary of burrow types and burrow contents encountered during the regular sampling at the Tooloom study site. The new generation of adults emerges in late summer from subterranean pupal balls in the previous season's nest burrows. These new adults initially form small individual burrows but then gradually pair up until, by the start of winter, virtually the whole population consists of pairs of beetles in larger burrows which they share for the rest of their life. In early spring the beetles start to forage out of their burrow for various items of vegetable detritus which are dragged down to the now-enlarged chamber at the end of the burrow. Foraging soon becomes the sole task of the male while the female remains in the burrow where she manufactures a 'brood mass' from the foraged material. In late September the female starts to construct small 'egg balls' from the brood mass and deposits an egg in each. Larvae hatch inside these tiny balls within a few days and this heralds a long phase of further foraging, brood mass manufacture, and progressive plastering of brood mass material on the outside of the enlarged brood balls which contain ever-growing larvae feeding from within. By mid summer most larvae are full grown and beginning to pupate within the now large balls which are constantly tended by the female. The male by now has ceased foraging and is excluded from the brood chamber of the burrow. Soon after, the new generation emerges by which time the original male and female are usually dead.

Detailed discussion of the various aspects of this life cycle is given under the following headings:

(i) BURROW DENSITY AND POPULATION SIZE. *Cephalodesmius armiger* occurs in a wide range of forest and soil types, and varies considerably in population density and size of individuals from locality to locality. The Tooloom study site was chosen because it was known to have a dense

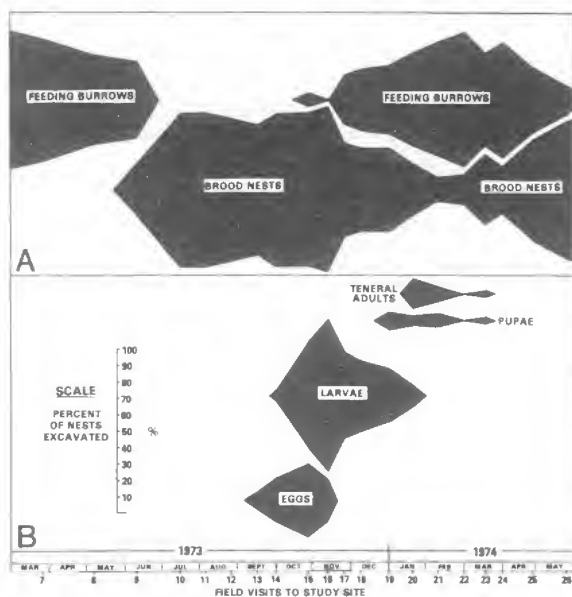


FIG. 1: Seasonal change in frequency of nest type (A) and in presence of life history stages in the burrows (B) of a population of *Cephalodesmius armiger* at Tooloom over a period of 15 months. Widths of the kite diagrams represent the percentage of burrows excavated on each field visit.

population of the largest form of the species known to us. An estimate of beetle density was made in August 1973 based on burrow entrances visible in 25 random 1 m² quadrats in each of two 1000 m² plots. In August the local population consists entirely of paired burrows (see Fig. 1) and hence the number of beetles can be assumed to be twice the number of active burrows. Plot 1 yielded an average of 2.4 burrows/m² (range 0–7) and Plot 2 had an average of 1.2 burrows/m² (range

0–3). Thus the population of this large scarab (12–15 mm length) on the Tooloom Plateau can be estimated at roughly 20 to 50 thousand beetles per hectare. The point to be made from these figures is that this large biomass of beetles is much greater than seems able to survive on mammalian droppings, the normal food source of the subfamily. The Tooloom region has a rather diverse mammal fauna (Calaby, 1966) but the species are mostly small and uncommon; the only species regularly encountered within the study area were the two small macropods, *Thylogale stigmatica* and *T. thetis*, and the two possums, *Pseudocheirus peregrinus* and *Trichosurus caninus*.

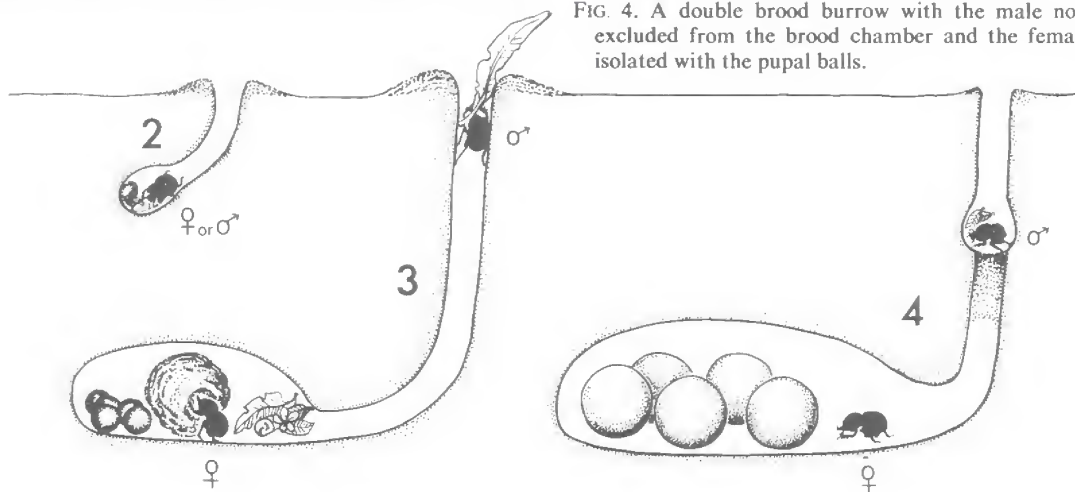
(ii) NEST STRUCTURE AND CONSTRUCTION. *Cephalodesmius* burrows are conspicuous on the forest floor at the study site and appear as vertical shafts with an open, circular entrance 10–12 mm in diameter, usually surrounded by a circular 'pushup' of soil brought to the surface by the beetles. Although the burrow entrances have a rather constant appearance all year round (Plate 2A) their subterranean structure varies seasonally. The main forms encountered are shown in Figs. 2–4.

FIGS 2–4: Types of burrows formed during different stages of the biology of *Cephalodesmius armiger*.

FIG. 2. Short feeding burrows made by newly emerged adults in late summer and occupied by single adults of either sex.

FIG. 3. Brood burrow constructed by a mated pair of adults. Shows the male dragging leaves into the nest and the female attending the brood mass she has manufactured from them. Five small brood balls containing developing larvae are shown at left.

FIG. 4. A double brood burrow with the male now excluded from the brood chamber and the female isolated with the pupal balls.



The simplest type is that made by the newly-emerging adults in late summer. These dig a short, sloping shaft 5–8 cm long which terminates in a small oval chamber not much bigger than the beetle itself (Fig. 2). These are invariably occupied by a single beetle of either sex and may also contain a few leaf fragments. They act as a short-term shelter for new adults before they pair off in autumn. We refer to these burrows as *feeding burrows*. In the field they decline rapidly in abundance by the end of May.

By early winter the great majority of burrows contain two adults, a male and a female, and these we have termed *brood nests*. They differ from feeding burrows in having a vertical entrance shaft, up to 10 cm deep, which turns and runs horizontally for 3–5 cm before opening into a large terminal chamber (Fig. 3). If the ground surface has any gradient the horizontal arm of these burrows invariably runs in the uphill direction. It is not known whether brood nest burrows result from modification of the feeding burrow of one sex after pairing has taken place or are excavated *de novo*. The terminal chamber of brood nests is slowly enlarged during the breeding season as the brood balls and brood mass become larger. It is not known whether one or both sexes are responsible for burrow enlargement, but observations of males scratching their fore tibiae and clypeal prongs against the solid plaster of the artificial nests indicate that the male may be the principal excavator.

In mid to late summer when brood balls are completed and foraging has finished, the male leaves the brood chamber and comes to reside in a small sub-chamber in the vertical shaft just below the ground surface. the remainder of the tunnel leading back to the brood chamber becomes filled with loosely compacted soil which effectively seals off the female beetle and her brood balls, most of which now contain pupae. This stage we have termed the *double brood nest* (Fig. 4). Careful probing is required to detect these double nests as they occur at a time when new season adults are emerging and forming feeding burrows with which double nests could be superficially confused. It is not known which sex causes the shaft blockage in double nests.

(iii) FORAGING BEHAVIOUR (Plates 1A, 1B, 2B, 2C, 2D, 3A, 3B).

Foraging forays outside the burrow form a major part of *Cephalodesmius* activity, especially

during the breeding season. Once the new generation has progressed from the initial feeding burrow phase to the paired brood nest phase it appears that the only reason adults leave the burrow thereafter is in search of food and brood mass material.

Foraging is principally a male activity. Females fend for themselves during the brief feeding burrow stage and during the early stages of the brood nest phase, but once brood mass manufacture starts the female rarely leaves the nest. This is shown by the preponderance of males among beetles intercepted outside the nest by both hand collecting and pitfall trapping during the major foraging period from August to January (Table 1).

Foraging for brood mass material is a daytime activity and takes place during periods of high humidity or direct moisture in the litter layer. Activity starts soon after dawn and continues while environmental moisture persists, usually until about midday. Light rain will stimulate commencement of foraging after it would normally have ceased and it is possible to artificially induce local foraging by sprinkling water on the soil. There is a certain amount of nocturnal foraging but this has some differences which will be discussed later.

Individual foraging sorties have a fairly constant pattern. The beetle emerges from the burrow and walks away from the entrance in a fixed direction with antennae extended and club segments opened wide. After examining several objects the beetle finally chooses one, picks it up with the forelegs, and backs towards the burrow entrance which may be up to a metre distant. Although the entrance may be obscured the beetle maintains an uncannily direct course — obstacles are crossed, not avoided, and a beetle will exert much time and energy in clambering up and over a large leaf rather than change course, e.g. Plate 2D. When the beetle is close to the burrow (within 5 cm) the foraged item is dropped while the beetle turns and walks *forward* towards the entrance. After briefly examining the entrance, apparently to test that it is the correct one, the beetle quickly returns to the foraged item and drags it backwards the remaining distance to the entrance and then down inside. With large items a considerable amount of pulling from inside is required before it is completely in. Rare occasions were noted when a forager tried to enter the wrong burrow and was actively pushed out by the occupant.

The great proportion of items taken into burrows were small leaves or leaf pieces, usually in a partly decayed state (Table 2). However, almost any soft organic matter was acceptable. Small flowers (e.g. *Claoxylon australe*) and fruits (e.g. *Melia azedarach*, *Diploglottis australis*) shed from the canopy trees were highly attractive to the beetles when seasonally available in the litter. *Diploglottis* fruits, although equalling the beetles themselves in size (Plate 2D), were taken into the burrows in large numbers and the soft flesh stripped from the seeds; one burrow (Visit 4) was found to contain 20 stripped seeds; other burrows were found in which multiple germination of the *Diploglottis* seeds had occurred, almost occluding the chamber. Occasionally living plants were attacked: at a steep site on Mt Clunie where litter had been removed by runoff, beetles were seen harvesting soft new shoots from vines on the forest floor. On Visit 23 at Tooloom several dozen beetles were encountered systematically cutting leaves from a newly fallen leafy branch of *Daphnandra micrantha*; individual beetles were seen to make several visits to the same branch, some travelling several metres beyond their normal foraging range to do so. *Daphnandra* is an aromatic plant with powerful alkaloids, and this may have stimulated this mass *Cephalodesmus* activity. The beetles readily took to various human detritus such as watermelon rinds and banana skins, from both of which they efficiently stripped the soft material. Where food material is fragmented before transport back to the burrow, as in the foregoing examples, the beetles use a combination of slashing movements of their saw-toothed fore tibiae and thrusting with their clypeal prongs.

The method used by *Cephalodesmus* to carry the foraged items has been described by Matthews (1974) who notes that it is not similar to that of any known scarabaeine. Objects are grasped by the fore tibiae and held tightly against the head region while the beetle walks backwards on the mid and hind legs. Heavy items, such as *Diploglottis* fruits, are transported by a series of dragging movements; the beetle reaches out as far behind as it can with the hind legs while retaining

a grip on the item with the extended forelegs. After getting purchase with the hindlegs all legs are contracted simultaneously thus dragging the object about a body length; this is then repeated.

Although plant material from the forest floor comprises the great bulk of material taken into the nests it is nevertheless true that animal dung is also occasionally gathered (Plate 3B). Table 2 records that recognizable dung pellets were found in 2.3% of the 426 burrows excavated during the study. Our observations on dung foraging, though sparse, indicate that this is a nocturnal activity and may primarily provide nutrients for adult beetles. At night beetles are often observed sitting at the tops of their burrows with antennae extended. Since most of the rainforest mammals in the study area are nocturnal this behaviour may enable early detection of dung pellets by the beetles. On several occasions pellets were noted lodged across the entrance to beetle burrows, and although too large to be dragged in, the beetle was tearing off portions from inside. When fresh bovine dung was exposed at night great numbers of beetles emerged to carry off portions. Pieces were separated from the main mass by pushing with the head and pulling with the forelegs while the whole beetle rotated; eventually a piece was torn free then dragged away backwards as for other items. No attempt is made to round off the piece after separation from the source. Foraging for plant material was never observed at night.

Artificial nest observations showed that foraging was a spasmodic activity. The male may go several days without foraging then commence a period of prolonged foraging for several hours until the nest chamber is almost filled.

(iv) PREPARATION OF BROOD MATERIAL. The materials dragged into the burrow by the male form the basic ingredients for the female to manufacture a processed, dung-like substance which is used both to make brood balls and as a food supply for adults. Brood mass manufacture starts in early spring (August) when the male begins serious foraging. Foraged items, predominantly leaves, are seized by the female and compressed with her forelegs until a tight mass is

TABLE 2: FORAGED MATERIAL FOUND IN 426 NESTS OF *CEPHALODESMIUS ARMIGER* EXCAVATED DURING STUDY VISITS TO TOOLOOM PLATEAU. FIGURES EXPRESSED AS PERCENTAGES OF TOTAL NESTS.

Empty	Leaves	Fruits	Seeds	Flowers	Leaf shelters of Attelabidae	Dung
35.6	57.7	1.6	4.9	3.0	1.4	2.3

formed. She constantly attends the mass, shaping squeezing and mashing it with her toothed tibiae and palpating its surface with her mouthparts. New material is compressed into its surface and the faeces of both the male and female are also added. As with all other Scarabaeinae the mandibles of *Cephalodesmus* are membranous and hence no chewing function is available to the female during preparation of the brood mass.

This brood mass grows slowly in size until it reaches three to four times the size of the female herself. By this stage the material has become dark in colour and fungal activity has commenced; almost invariably larvae of the phoretic sphaerocerid fly, *Leptocera myrmecophilia* (Knab and Malloch), are present, tunnelling through the medium. After about two weeks the brood mass reaches a uniform, mushy consistency, still with recognizable fibrous plant material present, but quite malleable. At this stage egg-ball construction may begin.

This final material bears a superficial resemblance to animal dung and Fricke's (1967) mistaken reference to a mass of 'horse-dung' in a burrow of *C. armiger* is quite understandable. That the beetles can prepare the final material entirely from plant matter is shown by the artificial nests which were fed no dung. In the field, new generation beetles start to process leaves into the brood material soon after digging their first feeding burrows and there is generally some brood mass present in the burrows right through the winter when foraging is minimal. This provides adult nutrient during winter but may principally be a mechanism to maintain the fungal flora through the non-breeding season. The mycology of the process needs investigation.

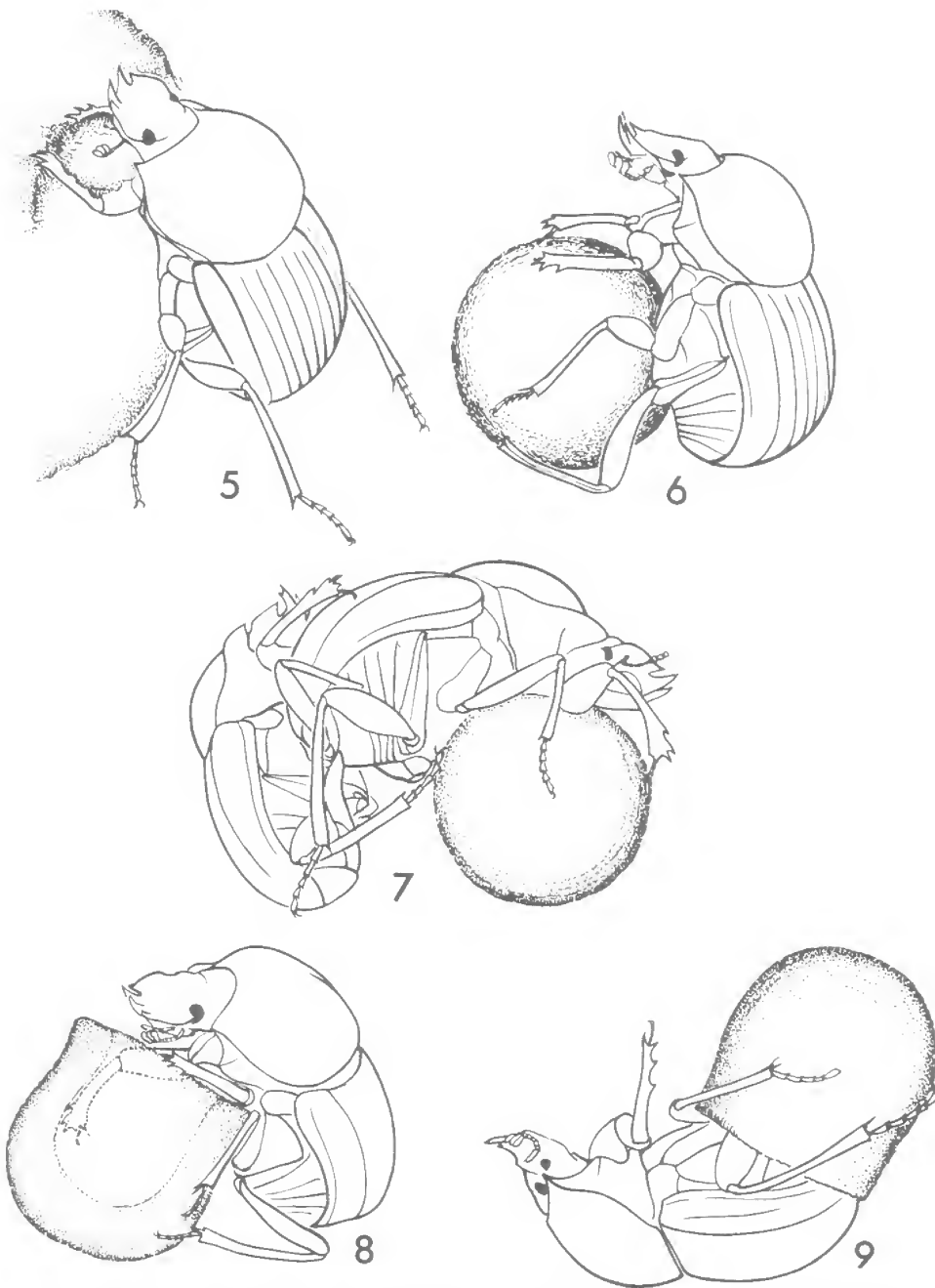
The brood mass apparently provides some nutrient for the adults because the female continuously licks its surface with the spongy lobes of her mentum and maxillae. The male often tries to feed on its surface also but is generally butted away by the female.

(v) EGG BALL CONSTRUCTION AND EGG-LAYING. The female reproductive system of *C. armiger* is normal for the Scarabaeinae in being reduced to a single ovariole on the left side, and the large (2–3 mm long), smooth, oval eggs laid are also normal for the subfamily. Eggs encountered during excavation of nests in the field were each enclosed loosely inside small (5 mm diameter), thin-walled, individual, spherical balls of brood material which we have termed egg balls.

Balls larger than these invariably contained larvae. These field observations posed two problems. Other known ball-rollers do not deposit the egg until sufficient brood material is accumulated for the larva to complete development. But it appeared that *Cephalodesmus* must add more brood material to the brood ball after egg deposition. In other words some degree of progressive provisioning must take place. And secondly, whereas normal ball-rollers have the simple task of depositing an egg in one end of a large ball of brood material, *Cephalodesmus* must possess additional manipulative skills to enable it to enclose its eggs inside fragile, thin-walled spheres of soft material. These problems were clarified by numerous observations on egg laying in the artificial nests.

Egg ball construction is solely a female task and commences once the brood mass has reached the correct state of decomposition. Using the forelegs the female first tears a small chunk from the brood mass (Fig. 5) and begins a long period of manipulation of it lasting up to three hours. Initially this is done in a 'sitting' position where the beetle rests on a tripod formed by the pygidium and the two hind legs (Fig. 6, Plate 2EF). Frequently the beetle topples over due to its activities and continues its manipulations while on its back or side. First the chunk of brood mass is rounded into a sphere using all pairs of legs, then it is turned, probed and licked for a considerable period while all the fibrous material and non-decayed leaf pieces are removed, retaining in the ball only the very fine homogenous substrate. During this phase the male may copulate with the female while she holds the ball (Fig. 7) (see Section vi). Regaining the sitting position, the female begins to hollow out the ball for reception of the egg (Fig. 8). The hollow is enlarged by inserting the forelegs further and further into the cavity, usually holding it steady with one fore tibia on the rim and the other inside pulling outwards to enlarge the cavity or scraping and smoothing the inner surface (Plate 3F). While this is in progress the ball is slowly rotated by the mid-legs giving a 'potter's wheel' effect ensuring uniformity of shape and wall thickness of the finished cup-shaped receptacle. This hollowing process lasts for approximately 30 minutes and the final shaped cup has a slightly flared rim.

Egg laying then takes place. The prepared cup of brood material is nimbly swung between the legs and clamped with its orifice over the abdominal apex and held in position by the mid- and hind-legs (Fig. 9). This lasts for 15–20



FIGS 5-9: Stages in egg-laying by a female *Cephalodesmius armiger*. Redrawn from photographs taken inside an artificial nest.

FIG. 5. The female tears a portion off the mass of cultured brood material.

FIG. 6. She forms it into a smooth sphere while in the 'sitting' position.

FIG. 7. The male approaches and copulates while the female works on the egg ball.

FIG. 8. The female hollows out the ball using the forelegs to form a lipped cup.

FIG. 9. Lying on her back she holds the cup over her abdominal apex and inserts an egg into the hollowed chamber. The opening is then closed and the completed egg ball rounded off.

seconds while an egg is deposited inside. The egg ball is then swung forward and its opening rapidly closed off by the forelegs. An additional 30–60 minutes are then spent in smoothing and rounding the completed egg ball.

Once a female commences egg laying she continues egg ball formation at the rate of approximately one per day until the full complement is reached. In the artificial nests this was between 10 and 12 balls but in field nests the maximum number observed was 7, with the usual number being 4 or 5. No further provisioning of brood material to the first egg balls takes place until the egg laying sequence is complete. Each female has only a single egg laying sequence in its lifetime.

(vi) COPULATION. Observations of copulation in the dung beetles are extremely rare and were reviewed by Halffter and Matthews, 1966. Halffter and Lopez (1977) subsequently studied copulation in *Phanaeus* (Coprini) and reviewed further literature. The great majority mate below ground in association with brood material, the only regular ground surface copulation being recorded in *Phanaeus*. Halffter and Lopez note that, in the Scarabaeini (to which *Cephalodesmus* belongs), mating has always been observed after brood ball construction, an exception being *Megathoposoma* (Wille, 1973).

Copulation was seen on several occasions in *Cephalodesmus armiger* and takes place under two different circumstances. The commonest is in the brood burrow at the time of egg ball construction. This activity appears to act as a behavioural cue for the male to commence copulation, since the male generally mounts the female while she is working on an egg ball (Fig. 7). Union usually lasts only a few minutes and is terminated by the female thrusting the male off. In some artificial nests copulation was noted on several consecutive days each time the female made a new egg ball. This indicates that copulation may be partly ritualized. In some nests no egg ball related copulation was seen.

Copulation also occurs on the ground surface in February–March. This is the period when the new generation is emerging and great numbers of both sexes may be found roaming outside the burrows in the daytime. On Visit 22 ninety foragers were collected at 10 a.m., of which two pairs were in copulation. One pair was an old generation male and a new generation female; the other pair were both new generation individuals. On Visit 23 thirty foragers were collected at 9.30 a.m.

including a new generation pair in copulation. Precisely a year earlier, on Visit 6, a new generation pair dug from a brood burrow were seen to copulate in their storage vial in the laboratory 36 hours after being excavated. These observations suggest that copulation may accompany pair bonding at the time when the new generation is in transition from the individual feeding burrow stage to the paired brood burrow stage in late summer. Such diurnal, above-ground mating unassociated with other breeding behaviour is unrecorded in the Scarabaeini and resembles that described by Halffter and Lopez (1977) for the Coprini genus *Phanaeus*.

(vii) PROGRESSIVE PROVISIONING OF BROOD BALLS. Eggs hatch within a week or so of deposition and the larva feeds on the inner surface of the egg ball as is usual in the Scarabaeini. The thin shell of brood material present in the original egg balls provides larval food for only a short period. Accordingly, additional brood material must be added to the outside of the balls to feed the growing larva inside. This post-eclosion, periodic feeding of progeny by the parents fulfils quite adequately the criteria of 'progressive feeding', a phenomenon usually confined to insects with advanced parental care, such as some Hymenoptera. It is common among ball-roller dung beetles for parents to tend and clean brood balls during larval development inside. But this added complexity in *Cephalodesmus* whereby the parents continue to manufacture brood material and progressively feed it to the developing larvae is unparalleled in the rest of the Scarabaeinae.

During this phase of larval growth inside the brood balls the parent male continues to forage plant material and the female continues to add it to the brood mass. However the process of adding brood material to the brood balls is entirely a female occupation. The male, when not foraging, merely rests immobile in the nest at the bottom of the exit shaft.

External provisioning of the balls does not commence until all egg balls are completed. Thereafter, all brood balls are periodically provisioned in turn so that at any given time all balls in a nest are roughly the same size. In the artificial nests excess balls are abandoned and destroyed during this early period of larval development. This presumably occurs in the field also, as the number of brood balls per nest is at its peak early in the season and then declines slightly later on. The brood material from these terminated balls appears to be returned to the

brood mass or added to other balls as all trace of them soon vanishes.

As the brood balls are enlarged the larvae within feed and grow at a proportionate rate so that the wall of the brood balls always remains at about 2 mm thick. During the later stages of larval development the female spends less time in processing foraged material. Larger larvae seem to be able to handle coarser material and bits of green leaf are often seen in the surface of larger balls. It is possible that some foraged material is added directly to the brood balls at this stage, rather than via culturing in the brood mass. However, brood mass is always present in the nest.

(viii) **LARVAL MORPHOLOGY AND BEHAVIOUR.** Halfpter and Matthews (1966) have summarized the remarkable behavioural and morphological adaptations which scarabaeine larvae exhibit for their life inside the spherical cavity of a brood ball. *Cephalodesmius* larvae conform well with all these features, viz. strongly arched body with a humped dorsum and truncate

abdominal apex for gaining purchase on the walls of the feeding cavity; progressive rotation during feeding so that ejected faeces are re-consumed together with new brood material; ability to rapidly seal off perforations in the wall of the brood ball with quick drying larval faeces. They differ from usual dung beetle larvae in being more strongly arched so that their head is almost always in close approximation to the abdominal apex (Fig. 11).

Edmonds and Halfpter (1978) give a detailed summary of larval morphology in the Scarabaeinae. They define the subfamily by 26 larval characters and give a key to the 25 genera whose larvae were available to them. *Cephalodesmius* larvae conform with the general subfamily pattern except that they lack the row of 'stridulatory' tubercles on the stipes, the raster on the last abdominal venter, and the transverse row of setae on the labium. They run to couplet 17 in Edmonds and Halfpter's Key where they do not fit comfortably with either *Copris* or *Arachnodes*. To enable *Cephalodesmius* to be compared with this

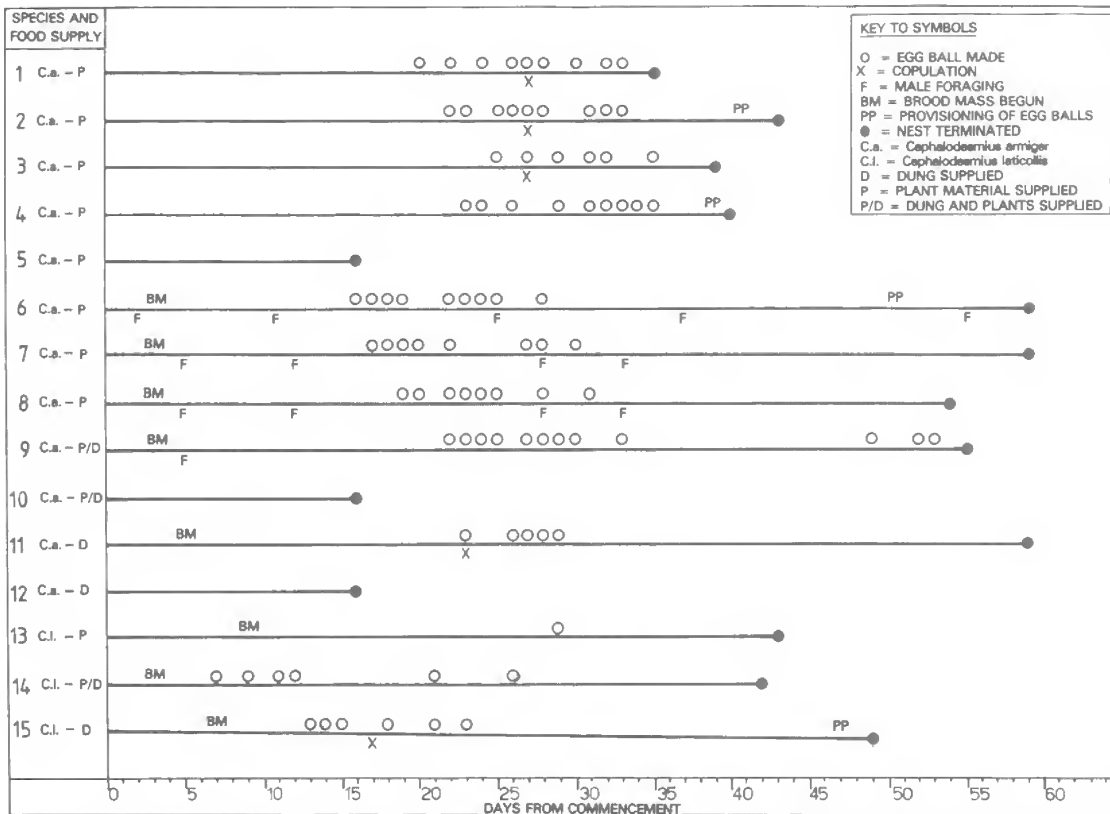


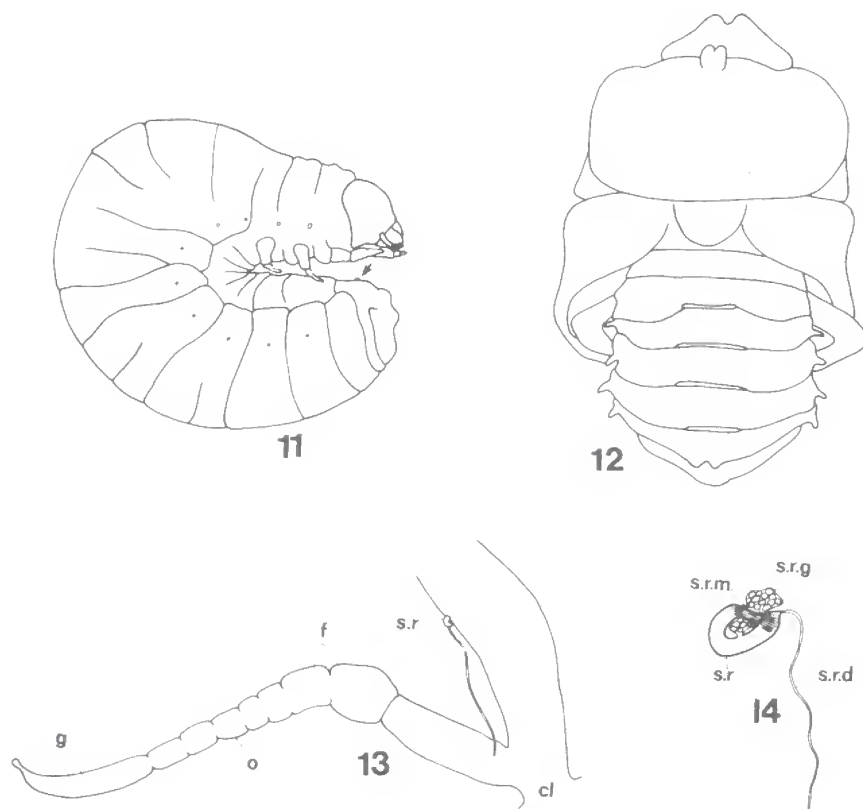
FIG. 10: Sequence of events in artificial plaster nests set up using mated pairs of *Cephalodesmius armiger* or *C. laticollis* dug from field nests.

study a brief description is given using Edmonds and Halffter's format and their paper should be consulted for explanation: (a) Sensory area of third antennomere conical; (b) chaetopariae with 3–4 setae; (c) lateral area of mandibles with two setae; (d) uncus of lacinia with a short, blunt basal tooth; (e) pronotal shields present but lacking produced anterior angles; (f) legs with terminal papillae; (g) third abdominal segment lacking a dorsomedian prominence; (h) last abdominal venter lacking a raster.

Cephalodesmius larvae agree with the genus *Sisyphus* in their lack of stipital tubercles and raster but can be easily separated from this genus and all other dung beetles by the remarkable stridulatory structures described in the following.

On several occasions during our study loud stridulations emanated from late stage larval balls of *Cephalodesmius armiger* after excavation from

field nests. These stridulations occurred when the balls had not been disturbed for some time and the sounds consisted of groups of rapid, short, sharp notes uttered at intervals of several minutes. Halffter and Matthews (1966) note that many scarab larvae of other subfamilies have an apparent stridulatory mechanism between the maxillae and the mandibles. For instance, larvae of the common Brisbane cetoniine, *Diaphonia dorsalis*, have a series of pegs on the anterior margin of the maxillary stipes which rub against a patch of ridges on the posterior margin of the mandible (pers. obs.). But Halffter and Matthews note that actual sound production by larvae has not been recorded in the family. Further, in the subfamily Scarabacinae this stridulatory mechanism is greatly reduced or, as in *Sisyphus*, absent. Such a maxillomandibular stridulatory device is also absent in *Cephalodesmius* but examination



FIGS 11–14: Immature stages and internal anatomy of *Cephalodesmius armiger*.

FIG. 11. Side view of larva removed from a brood ball. The position of the stridulatory structure on the last abdominal sternite is arrowed.

FIG. 12. Dorsal view of pupa, showing supporting processes on prothorax and abdomen.

FIG. 13. Reproductive system of female.

FIG. 14. Detail of the seminal receptacle. Abbreviations: cl., cloaca; f., follicle; g., germarium; h.g., hind gut; o., ovariole; s.r., seminal receptacle; s.r.d., seminal receptacle duct; s.r.gl., seminal receptacle gland; s.r.m., seminal receptacle muscle.

revealed a quite novel stridulation arrangement. It consists of a large, sub-rectangular, well-sclerotised region of the gular part of the head (Plate 3C) which bears about 45 fine transverse ridges (the stridulitrum in the terminology of Ashlock and Lattin 1963) (Plate 3E); against this rubs a small, midline sclerotization of the last abdominal sternum bearing several transverse flanges (the plectrum; Plate 3D, F). This mechanism occurs in all three instars of *Cephalodesmius armiger* as well as in the few larvae of *C. quadridens* and *C. laticollis* available to us. This sort of stridulation, where the two soundproducing components are at opposite ends of the body, and where the animal has to scratch its 'chin' with its 'tail', as it were, is believed to be unique in the insects. Dung beetle larvae, with their head permanently approximating their abdomen, are one of the few animals predisposed to the evolution of such an arrangement.

The functional significance of this stridulation behaviour in *Cephalodesmius* can only be guessed at. It is unlikely that it is of alarm or defense function because it was never heard when nests were being excavated or when balls were being handled. However, the close association between the mother beetle and the larval balls during the process of progressive provisioning suggests that stridulation may be a form of communication between the larva sealed inside the ball and the female. The female has no obvious way of detecting the rate of larval feeding inside the ball, and yet opened balls from excavated nests have remarkably constant thickness of brood material surrounding the feeding larva inside. This suggests that the larva communicates wall thickness to the female; in other words, larval stridulation in *Cephalodesmius* may be just the age-old cry from progeny to parent: 'Bring more food!' No stridulation was observed in adult *Cephalodesmius*.

(ix) PUPATION AND PUPAL MORPHOLOGY.

The growing larval brood balls reach a maximum of 16–18 mm diameter after which provisioning by the parent female ceases and the larva inside soon pupates. At this stage the male stops foraging and becomes sealed off from the nest chamber by a blockage of the entrance shaft. This is the double brood nest stage (see Section ii). The female remains in the inner chamber with the pupal balls.

In the later stages of progressive provisioning of the larval balls their surface is coarse and fibrous because of the incomplete decomposition of the brood material being added. By contrast the shell

of the final pupal balls consists of hard, dark material of very fine texture; the problem of its origin arises. Halffter and Matthews (1966) summarize some observations, especially those of Siyazov (1913) which suggest that the pupal ball shell in some dung beetles may be formed, at least in part, by the faeces of the larva itself. Although our artificial nests did not survive to the pupal stage, and thus direct observations are not available, there is strong evidence that this is also the case in *Cephalodesmius*. Larvae of all ages have the capacity to produce large volumes of liquid faeces which is used to repair accidental holes in the brood ball. The grooming activities of the female parent soon smooth away any external evidence of these repairs. But towards the end of larval growth the amount of larval faeces being ejected from the ball far exceeds that expected in response to accidental ball perforations. For example, if large larval balls dug from field nests are isolated from the female parent for a few hours they become covered with large clots of ejected faeces. On the other hand, if similar balls are confined with the female these clots do not form because they are being continually smoothed over the surface by her. This suggests that when the near-mature larva is consuming the last of the accumulated brood material from the inside surface of the ball it is simultaneously evacuating the undigested residues from its alimentary canal to the exterior of the ball where they are spread by the female and solidify to become the fine-grained, dark material of the pupal shell.

Dung beetle pupae are distinctive in possessing dorsal and/or lateral projections on various of the body segments. These support the pupal body above the inner surface of the pupal ball (Halffter and Matthews, 1966). Edmonds and Halffter (1978) coin the term 'pupal support projections' for these structures and review their distribution among the genera known to them. Pupae of *Cephalodesmius armiger* (Fig. 12) have weak development of pupal support projections and lack the very long, filamentous structures seen in many species; however they possess the full complement of projections which Edmonds and Halffter list as constant in the subfamily as follows: (a) Pteronotal projections — both mesonotum and metanotum bear small, median papillate projections; (b) Lateral tergal projections occur as distinct finger-like lobes on segments 3, 4 and 5 becoming less distinct on segments 6 and 7; (c) Dorsal tergal projections — the median longitudinal fold is weakly developed and replaced functionally by transverse raised folds on most

abdominal terga; (d) Caudal projection takes the form of a thickened tergal area only. In addition to these a prominent, bilobed, pronotal projection is present.

(x) EMERGENCE AND BEHAVIOUR OF NEW ADULTS. Pupal life is relatively brief, probably of the order of 2–3 weeks. Although direct measurement of pupal period was not possible it can be seen from Fig. 1 that in the field the first teneral adults inside balls occurred only 19 days after the first pupae were encountered. All pupae have emerged by the end of March at Tooloom.

Teneral adults remain inside the pupal balls for a few days while hardening takes place. When they break out of the balls they apparently leave the burrow almost immediately since tenerals were never found free inside the nest chamber. Their exit route is by way of the original entrance burrow since extra exit holes from post-pupal brood chambers were never found. By this stage the original parent female is usually dead and her body was often found in such abandoned nests. The fate of the parent male is uncertain because all trace of him has gone after the exit of the new adults via the secondary chamber he occupied during the double nest phase (Fig. 4).

The new generation adults dig and occupy small individual feeding burrows soon after they emerge from the parent nest. These short, temporary burrows are soon stocked with a few leaves. During this period large numbers of both sexes appear on the ground surface on favourable days (Table 1, Visits 21, 22, 23). While much of this surface activity is undoubtedly concerned with foraging, the incidence of daytime copulation (Section vi) suggests that mate selection also takes place leading to the formation of paired brood nests which rapidly supplant the single feeding burrows.

(xi) OVERWINTERING ADULTS. By the onset of cold weather in April/May almost all burrows are paired brood burrows each containing a new generation male and female (Fig. 1). The terminal chamber is moderately enlarged but usually contains several small leaf pieces and no brood mass. This situation persists through winter.

No daytime foraging was noted in winter but pitfall trapping continues to yield some adults during the coldest months (Table 1). This probably indicates nocturnal foraging by adults for faecal food for themselves; it is significant that these pitfall catches include both sexes. It was a

common observation to find adults at night sitting at the entrances to their burrows with head and extended antennae protruding. Occasional instances were noted where a pademelon (*Thylogale* sp.) dung pellet had been pulled across the entrance to a burrow while the beetle tore away at it from the inside. Since pademelons are entirely nocturnal these observations suggest that the beetles wait at their burrow entrance to sense newly deposited pellets in their vicinity.

Towards the end of winter further enlargement of the terminal chambers takes place, indicated by the appearance of fresh soil pushups at burrow entrances. Then in early August foraging for plant material starts in earnest and soon brood mass manufacture by the female heralds the start of a new reproductive cycle.

(xii) NATURAL ENEMIES. *Cephalodesmius armiger* appears to have few natural enemies despite its large population size. Diurnal foragers would appear to be vulnerable to bird predation, but this was never observed. Foraging adults freeze for several minutes in a rigid, often ungainly, posture when disturbed and this, together with their soil-like colour, affords them considerable cryptic defence.

Few predators enter the underground nests. Of the more than 400 nests excavated active predation was noted on only three occasions. Twice at Tooloom large geoplanid planarian worms were found attacking the nest inhabitants, and once at Lever's Plateau a tenebrionid beetle (*Otrintus cylindricus* Carter) was found with partly consumed adult *Cephalodesmius*. Occasionally nests invaded by fungus were found but it was not clear if the fungal invasion had followed nest death from other causes. The only case of vertebrate excavation of nests was noted at Victoria Park, near Lismore, in December 1974, where a considerable number of nests had been dug up and the adults and larval balls eaten; this is presumed to have been the work of bandicoots (*Perameles* sp. or *Isoodon* sp.).

In late summer and autumn numerous dead adults may be found on the ground surface but this appears to represent natural mortality of the previous year's generation after emergence of their progeny.

A female from Tooloom (Visit 14) dissected for ovary inspection contained numerous encysted nematodes in the body cavity. This suggests that, like many other scarabs, *C. armiger* may act as the intermediate host for a parasitic worm.

(xiii) NEST INQUILINES AND PHORETIC ASSOCIATIONS. The stable, humid environment of *Cephalodesmius* nests and the rich supply of organic material stored therein eminently predisposes them to exploitation by other organisms. During field observations a number of other arthropods were encountered in the nests or on the bodies of the beetles and some were found to have entered into rather intimate associations with their hosts. A more detailed account of the biology of these species and their interaction with *Cephalodesmius* will appear later (Monteith, *in prep.*) but for completeness a brief, annotated list of the more important species is given here. The taxonomy of the mite fauna has already been investigated (Costa, 1975).

ACARINA—MESOSTIGMATA

Family Macrochelidae

Macrocheles tenuirostris Krantz and Filippini, 1964. A sluggish mite commonly found clinging to adults of *C. armiger*.

Family Laelapidae

Hunteracarus womersleyi Costa, 1975. An active, abundant mite found clinging to the adult beetles and occasionally free in the nest.

ACARINA—ASTIGMATA

Family Anoetidae

Histiostoma sp. A minute, white mite which feeds and proliferates on the outer surface of the brood mass. It has phoretic hypopial stages which attach to the integument of adult *C. armiger*.

Family Acaridae

Caloglyphus sp. This minute white mite with long dorsal hairs built up to considerable numbers among leaf fragments in *C. armiger* nests. Like *Histiostoma* sp., its hypopi were phoretic on the adult beetles.

INSECTA — COLLEMBOLA

Family Entomobryidae

Sinella sp. This springtail was often encountered in numbers in nests of *C. armiger*.

INSECTA — COLEOPTERA

Family Staphylinidae

Anotylus sp. n. This rove beetle habitually bred in the nests of *C. armiger* and its adults and larvae could be found burrowing through the brood mass. Adult *Anotylus* have a phoretic association with the adult scarabs and were often found clinging to the dorsum of

foraging beetles (Plate 1B). This 'kleptoparasitic' relationship is referred to by Hammond (1976).

Oxytelus sp. This species belongs to the same subfamily as *Anotylus* sp. It was taken on several occasions in nests of *Cephalodesmius quadridens*.

INSECTA — DIPTERA

Family Sphaeroceridae

Leptocera myrmecophila (Knab and Malloch) Larvae of this fly were almost invariably found tunnelling through the brood mass of *C. armiger* nests and adults were often found free in the nests. The adults were also strongly phoretic on the adult beetles and were frequently seen riding foragers back to their nests (Plate 2B, 2C, 2D, 3A).

(xiv) OVARIAN CYCLE. The Scarabaeinae show the most extreme ovarian reduction known in the Coleoptera. All 38 species studied to date have only the left ovary present, and this is reduced to a single ovariole (Robertson, 1961; Ritcher and Baker, 1974; Halfpter and Lopez, 1977). This was confirmed for *Cephalodesmius laticollis* by Matthews (1974) and that of *Cephalodesmius armiger* is similar (Fig. 13). Its seminal receptacle (Fig. 14) is of the advanced type with the chamber strongly arched and provided with muscles on one side only (Halfpter and Matthews, 1966).

Dissection of female beetles collected on each of Visits 4–18 over a period of 12 months showed a pronounced cycle of ovarian activity. No developing egg follicles appear in the ovariole tubes until mid-July, about six weeks before the start of egg-laying in the field. By late August, almost all females have developing follicles. These may number up to 10, which is in contrast to the general tendency in dung beetles for follicle reduction. This appears to accord with the observed pattern of egg production in *Cephalodesmius* where eggs are produced in one-a-day succession for a number of days until egg-laying ceases. By the beginning of December all ovaries are spent.

(xv) RELATIONSHIP WITH MICROFLORA. Halfpter and Matthews (1971) have summarized recent studies which indicate that dung beetles have a complex gut flora of saprophytic and cellulose-digesting organisms which aid their utilization of the plant component of their dung food. This aspect of *Cephalodesmius* biology was not investigated in the present study. However

some of our observations indicate that there may be a complex process operating whereby gut-transfer of a fungal organism is effected.

All pupal balls opened during our field sampling were found to have several fungal fruiting bodies projecting from the wall into the pupal chamber. Each fruiting body consisted of a conical base bearing an apical, white spore-body. These delicate fruiting bodies must grow into the interior of the ball after the larva has ceased feeding and has completed the pupal ball by evacuation and solidification of its own faeces (see Section ix). When balls containing hatched, teneral adult beetles were opened, however, these fruiting bodies were invariably missing or truncated. The suspicion that these newly emerged adults had made their first meal of the fungal bodies was confirmed by examining the gut contents of the beetles. It is tempting to speculate that this is a mechanism which enables gut transfer of symbiotic fungus to the new generation of adults. Bearing in mind that these adult beetles later combine their own faeces with the brood mass manufactured from foraged leaves (see Section iv) it is easy to see how this mechanism could effect transfer of the specific fungus used to culture mashed leaves into dung-like brood material. Experimental proof of this apparent transfer process will be of great interest.

NOTES ON OTHER SPECIES OF *CEPHALODESMIUS*

The other two species of *Cephalodesmius* both occur in the same general region where the main studies were carried out. *C. laticollis* is the largest species, reaching 17–19 mm in length, and has a restricted distribution in the red soil rainforests of the Lamington, Tamborine and Springbrook plateaus; Matthews (1974) gives an unconfirmed record for the Dorrigo plateau in New South Wales. *C. quadridens* is the smallest member of the genus, reaching 5–7 mm, and shows sufficient geographic variability that more than one species may be involved (E. Matthews, *pers. comm.*). It is more widespread than *laticollis* and is most abundant in the drier, western part of the generic range. Most rainforest tracts were found to be occupied by two *Cephalodesmius* species and all combinations occurred. At Tamborine, the *laticollis/quadridens* combination occurred at Lamington and Wiangaree *laticollis/armiger* shared the rainforest floor; and *armiger/quadridens* coexisted at Tooloom, Mt Glorious and Bunya Mountains. At no single site were all three species encountered.

During the course of our studies on *C. armiger*

sufficient observations, both in field and laboratory, were made on *laticollis* and *quadridens* to show that they share the same pattern of nest formation and leaf utilization. These are summarized as follows:

(i) *Cephalodesmius laticollis*. This species constructs nests similar to those of *C. armiger* except that the entrance shaft may spiral. The terminal chamber may be as large as a clenched fist. Adults forage in the daytime for both dung and leaves. Dung was found in the nests more often than for *C. armiger*. *C. laticollis* was maintained in artificial nests, but less successfully than for *C. armiger*. However brood mass manufacture and egg ball construction was seen to be similar to that described in *armiger*. In the field, *laticollis* started making egg balls as early as the end of May at Beechmont, much earlier than the Tooloom population of *armiger*. Burrows with full grown larvae were found in October, and empty burrows in December. Thus, there is apparently still only one generation per year, with larval development in winter–spring, rather than spring–summer as in *armiger*. Up to 5 brood balls per nest were found.

(ii) *Cephalodesmius quadridens*. Nests of this small species were excavated at Mt Tamborine, Mt Glorious, Benarkin and the Bunya Mountains. They usually conform to the normal pattern of a vertical shaft and a horizontal, terminal chamber but frequently are under the edge of logs or stones on the ground. None were kept in artificial nests. Though *quadridens* comes commonly to nocturnal, dung-baited pitfall traps all nests examined (over 45) contained only leaf and other plant material. No foraging adults were observed and this may be explained by their small size, or perhaps by nocturnal habits. The life cycle appears shorter than that of the other two species. Egg balls were found in October and teneral adults in December but there is no evidence of more than one generation per year. Up to 9 brood balls per nest have been found. Pupal balls opened at Bunya Mountains in January had fungal fruiting bodies projecting into the chamber as were described for *C. armiger*. An intimate fungal relationship is thus also suggested in *C. quadridens*.

DISCUSSION

As can be seen from the recorded observations both in the field and in laboratory nests, *Cephalodesmius* has a remarkable biology, undoubtedly one of the most complex in the Scarabacinae. It also exhibits many unique

features found nowhere else in the subfamily. Plant material is used for adult feeding and nidification, with a dung-like substance being formed from it. Pair bonding and residence in a single burrow are longer than recorded for any other dung beetles. Parent to offspring bonds are also stronger, indicated by the novel method of larval stridulation. *Cephalodesmius* is also the only known scarabaeine to exhibit progressive provisioning of the larval food supply.

The use of processed plant material for nidification is unique in the Scarabaeinae, both in the material used and in the manner in which it is converted to a dung-like substance. Most records of dung beetle genera in decomposing vegetable matter cited by Halffter and Matthews (1966) are small species taken in leaf litter samples without any indication that they actually utilize the litter itself. The use of fruits is much better substantiated, with some species such as the Australian *Onthophagus vilis* Harold apparently relying on this sort of medium exclusively for adult and possible larval food (pers. obs.). Even in these species no processing is involved, the decaying fruit merely replaces dung as the food supply.

Permanent pair bonding and residence within a single burrow for the lifetime of the pair are also interesting features of their biology. According to Halffter and Matthews (1966), scarabaeines normally form pair bonds only for the period of nidification, or less. In *Cephalodesmius*, pair bonding extends for almost a year from the short feeding phase until the death of the pair. In the Scarabaeinae the length of burrow occupation by the adults varies. In some (e.g. *Onthophagus*) the female alone is involved in provisioning and stays in the burrow only until egg-laying is complete. In others, such as Halffter's (1977) nidification Groups III and V, females, and sometimes the male also, show brooding behaviour, attending the brood balls for part or all of their development. Again, this brooding period in *Cephalodesmius* is the longest of all Scarabaeinae, with both male and female resident continuously.

Cephalodesmius is the only scarabaeine known to exhibit progressive provisioning of the larval balls. In all other genera, the developing larva is provided with enough food to complete development at the time the egg is laid (Halffter, 1977). This results in a very close bond between the female and the developing larva which she, in fact, never sees or touches. Hence the development of communication via the unusual larval stridulation mechanism, another illustration of the close

relationship of individuals in a *Cephalodesmius* family. This is a truly subsocial relationship, certainly the most complex yet described in the subfamily, and one of the most advanced in the Coleoptera.

The repertoire of manipulative skills in the female *Cephalodesmius* exceeds that of other known scarabaeines. Many of these have no analogous equivalents in normal dung beetles and it must be assumed that many evolutionary steps have led to the intricate mechanisms we see today. These include the procedures of mashing leaf material into brood mass substrate, the process of plastering thin layers of brood material on to the growing brood balls, and, most complex of all, the fashioning of fragile, hollow, egg-ball shells from the brood mass.

So many aspects of *Cephalodesmius* biology are anomalous within the context of known dung beetle behaviour that it is difficult to place the genus into generally accepted evolutionary schemes. The use of leaf material for larval food is not known elsewhere in the Scarabaeinae, but does occur in some Geotrupinae, a subfamily regarded as a primitive relative of the true dung beetles (Ritcher, 1958). Some geotrupines use surface humus or decaying leaves as brood material (Howden, 1955). In particular, the genus *Lethrus* has many parallels with *Cephalodesmius* in that males bring fresh leaves to females in burrows who prepare balls of masticated leaves from them which are used to provision larval cells; the larvae consume the leaf material after it has been invaded by fungal hyphae (Nikolayev, 1966). Now the tribe to which *Cephalodesmius* belongs is generally considered primitive so the question obviously arises as to whether the diet of dung-like, processed leaf material in *Cephalodesmius* is a precursor to true dung feeding in the subfamily. Most evidence, however, indicates that the feeding habits of *Cephalodesmius* should be regarded as specializations on an original coprophagous stock. All the normal modifications of the Scarabaeinae for dung feeding and nidification are present: atrophy of adult mandibles; ability to transport food items, dig nests and prepare spherical brood balls; modification of larval morphology and behaviour for life inside a spherical food source. This seems particularly significant with respect to the adult mouthparts. The Geotrupinae have chewing adult mandibles, and these are used for leaf cutting and mastication in leaf culturing forms such as *Lethrus*, but *Cephalodesmius*, having lost the chewing function, has been forced to develop

alternative mechanisms of leaf harvesting and mastication using its tibiae and clypeal prongs. It is doubtful if this would have come about if *Cephalodesmius* had not developed from a dung feeding ancestor. The occurrence of incipient dung feeding in adult *Cephalodesmius* should probably be interpreted as retention from previously more extensive use of dung in the diet. While it is difficult to conceive that a litter feeder, with its almost limitless food supply, should need to learn to utilize the rare dung pellets as food, it is reasonable to assume that an originally obligate dung feeder might undergo a dietary shift into the more abundant litter but retain facultative use of some dung food, perhaps as a protein source for egg maturation in adults.

The subtribe Canthonina to which *Cephalodesmius* belongs, contains many species which construct multiple brood balls from dung which they transport to underground nests (Halffter, 1977). For the reasons given above we believe that *Cephalodesmius* should be regarded as derived from one of these multiple nest canthonines which initially learned to augment its dung supply by mixing in soft plant material and later became so successful at utilizing this material that it was able to forgo the use of animal dung almost completely.

Halffter (1977), in a discussion of the evolution of nidification in dung beetles, distinguishes six basic groups of nesting patterns and strategies. His Groups I to III are variations on the nesting strategy where food is buried in nests at the food source and his Groups IV to VI cover those that transport food away from its source before digging the nest (the ball-rollers). On the basis of preliminary information on *Cephalodesmius*, Halffter included it, with the taxonomically unrelated subtribe Coprina, in his Group III, which comprises species which make multiple brood balls in a previously excavated gallery and then exhibit parental care. In doing so Halffter dissociates *Cephalodesmius* from the rest of the Scarabaeini which are divided between Group IV (ball-rollers with single ball nests and no parental care) and Group V (ball-rollers with multiple balls and parental care). In this system *Cephalodesmius* is split from its relatives because it does not find food then transport it in search of a nest site as do normal ball-rollers, but rather it builds a nest before actually gathering food. When we consider why this is so it becomes clear that this behavioural anomaly in *Cephalodesmius* is better explained as an unusual Group V pattern than as grounds for transferring it to another

group altogether. The food of normal dung beetles, whether it be dung, carrion or fungi, occurs as discrete masses spatially separated in the environment. The beetles must search actively to find one of these food masses before any brooding behaviour, such as nest excavation, can begin. By contrast, the leaf litter food of *Cephalodesmius* is uniformly and abundantly distributed over the forest floor and thus *Cephalodesmius*, alone among dung beetles, can afford the luxury of dispensing with food searching before brood burrow construction; in fact the brood burrow is made some months before breeding activity starts in the assumption that food will be available when required. It should be noted that when brood foraging commences the ball-roller strategy of transporting food items across the ground surface to the nest site is used. The Coprina of Halffter's Group III bury brood material at the food source. For these reasons, *Cephalodesmius* seems more comfortably accommodated with its taxonomic relatives in Group V of Halffter's evolutionary schema.

Several aspects of *Cephalodesmius* biology merit closer examination than has been possible in the present study. These include the relationship between the beetles and their phoretic associates, the role of fungi in brood material formation, the mechanism of fungal transfer between generations, communication between larvae and adults, the extent and significance of dung feeding by adults, and the relative roles of the sexes in burrow excavation. These intriguing beetles have already proved themselves remarkable, but clearly have many behavioural phenomena yet to be fully understood.

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MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE I.

- A. Foraging male of *Cephalodesmius armiger* carrying a dead leaf backwards towards its burrow.
- B. Foraging male of *C. armiger* with two specimens of a phoretic staphylinid beetle (*Anotylus* sp.) clinging to its dorsum. The staphylinid breeds in the brood mass in burrows of *C. armiger*.

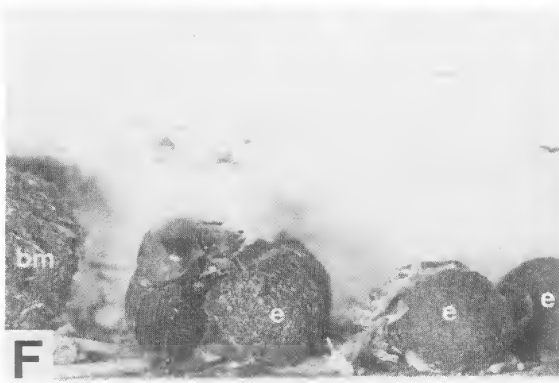
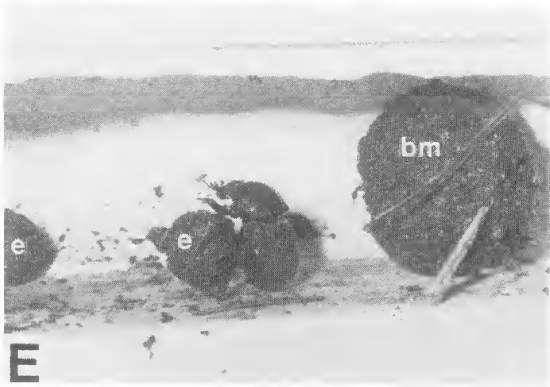
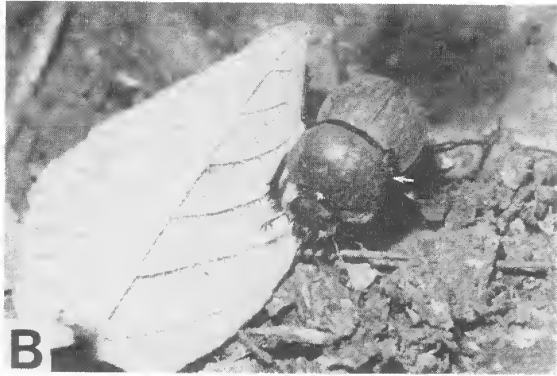


MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 2.

CEPHALODESMIUS ARMIGER

- A. Typical brood burrow in forest floor showing 'pushup' of soil surrounding entrance.
- B. Foraging male about to drag a green leaf into burrow entrance. Beetle carries a phoretic fly, *Leptocera myrmecophila*, on its prothorax.
- C. Foraging male with phoretic *L. myrmecophila* riding on its back.
- D. Foraging male drags a fallen *Diploglottis* fruit over the edge of a leaf. Two phoretic flies ride on the fruit.
- E. Interior of a plaster artificial nest showing a female beetle shaping a piece of the brood mass (bm) into a sphere which will become an egg ball.
- F. Female beetle hollowing out the inner cavity of a partially finished egg ball (c). Two completed egg balls and the brood mass (bm) are visible.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 3.

CEPHALODESMIUS ARMIGER

- A. Foraging male dragging a piece of dead leaf. Phoretic flies, *Leptocera myrmecophila*, ride on the leaf and on the head and thorax of the beetle.
- B. Seven beetles working at night at Tooloom on dingo faeces.
- C. Stereoscan of ventral view of larval head showing area of stridulatory ridges on gula (g).
- D. Stereoscan of last abdominal sternite of larva showing convex stridulatory structure which opposes the gular ridges of the head. Position of the anus (a) is shown.
- E. Detail of gular ridges.
- F. Detail of sternal stridulatory structure.

